

THE TAMARICACEAE IN THE SOUTHEASTERN UNITED STATES¹

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TAMARICACEAE Link, Enum. Hort. Berol. **1**: 291. 1821, "Tamariscinae,"
nom. cons.

(TAMARISK FAMILY)

Small trees or shrubs [subshrubs] of temperate and subtropical deserts, steppes, and shorelines, on sands, clays, and saline soils. Wood ring-porous or semi-ring-porous; sieve-element plastids of the S-type. Branches slender, persistent or deciduous. Root systems variable, ranging from taproots with relatively short lateral roots to extensively branched, horizontally spreading roots (branches when buried often also producing adventitious roots). Leaves scalelike or small, alternate, simple, entire, usually sessile [rarely subpetiolate], exstipulate, subimbricate, [amplexicaul in some species of *Tamarix*], often fleshy or punctate, with salt-secreting glands, usually glaucescent, with sclereids consistently present at or near vein endings; stomata anomocytic, on both surfaces of leaves

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The illustration of *Tamarix* was prepared by Karen Stoutsenberger from dissections by Kenneth R. Robertson and Carroll Wood from material collected by R. E. Ueber (614, GH; along the Rio Grande west of Mountainair, Socorro Co., New Mexico), R. L. Wilbur (7173, GH; Carteret Co., North Carolina), and D. S. Correll and H. B. Correll (9599, GH; Cameron Parish, Louisiana).

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[only on abaxial surface in *Myricaria germanica*]. Inflorescences spicate or racemiform, often aggregated in terminal panicles [or flowers solitary in *Hololachna* and *Reaumuria*]. Flowers perfect [2 species of *Tamarix* dioecious], regular, small, hypogynous, 4- or 5- [6-]merous; pedicels subtended by small, scalelike bracts. Sepals 4 or 5 [6], free or slightly connate, persistent, imbricate. Petals 4 or 5 [6], alternating with and larger than sepals, free, sometimes persistent [with a pair of ligular appendages near base in *Reaumuria*], inserted at base of a fleshy or membranaceous disc, imbricate. Stamens 4 or 5 [to 10 in *Tamarix*, to 75 in *Reaumuria*], usually haplostemonous or obdiplostemonous, usually free [monadelphous in *Myricaria*, fasciculate in 5 bundles in *Reaumuria*]; filaments filiform; anthers tetrasporangiate, 2-locular, versatile, extrorse in *Tamarix* [introrse in *Myricaria*], longitudinally dehiscent, slightly longer than wide; pollen (2-) 3- (4-)colpate, simple or in tetrads, binucleate (in *Tamarix*) [trinucleate in *Myricaria*]. Gynoecium of (2) 3 or 4 (5) carpels united in a compound, superior, unilocular ovary; placentation parietal, placentae sometimes intruded, making the ovary appear plurilocular near base and apex, or reduced, making placentation appear basal; styles 3[-5], distinct or connate at base; stigmas apical or decurrent adaxially [sessile in *Myricaria*]; ovules 2 to many on each placenta, with short funiculi, erect, anatropous, bitegmic, crassinucellar. Fruit a loculicidal, pyramidal capsule, the 3[-5] valves placentiferous at base, coriaceous; seeds long-pilose over entire surface [Reaumurieae] or at apex only, with unicellular hairs, which may be prolonged into a conspicuous hygroscopic coma (Tamariceae), micropyle formed by endostome; endosperm with development nuclear [cellular in *Tamarix tetrandra*], degenerating quickly in Tamariceae [persistent in Reaumurieae]; cotyledons 2, oblong, obtuse at apex, flat or plano-convex, the radicle short, conical, inferior; megagametophyte (embryo sac) tetrasporic, but postmeiotic development variable, usually Fritillaria or Adoxa type, embryogenesis of Solanad type, with broad, massive suspensor formed, polyembryony occasional. Base chromosome number 12. (Including Reaumuriaceae Ehrenberg.) TYPE GENUS: *Tamarix* Linnaeus.

A relatively small family of five genera (*Hololachna* Ehrenb., *Myricaria* Desv., *Myrtama* Ovcz. & Kinz., *Reaumuria* L., and *Tamarix* L.) and about 100 species, occurring primarily in central Asia, the Middle East, northern Africa, and the Mediterranean region of Europe. Several species of *Tamarix* have been introduced into North America, and six of these have become naturalized in the Southeast.³

The Tamaricaceae are one of numerous families that have been placed in the catchall order Parietales. Other early suggestions of relationship included the Guttiferales (Endlicher; Grisebach; Hallier, 1911), Rutiflorae (Caruel), and

³*Myricaria germanica* (L.) Desv. has been cultivated in the Southeast. The following key will allow its identification in the event that it is discovered as an escape.

Filaments free, inserted on a disc; anthers extrorse; our species with 4 or 5 stamens. . . . *Tamarix*.
 Filaments fused into a membranaceous tube (monadelphous); anthers introrse; stamens 10. . . .
 *Myricaria*.

Centrospermae or its segregates (Adanson; Bessey; De Candolle; Hallier, 1903; Jussieu; Saint-Hilaire; Vesque).

In most recent ordinal classifications, the families of the Parietales have been redistributed, and the Tamaricaceae are now generally placed in the small order Tamaricales, along with the Frankeniaceae (Thorne, 1976) and/or Fouquieriaceae (Barkley; Behnke; Bentham & Hooker; Boivin; Hutchinson, 1964; Takh-tajan, 1980), or in the larger order Violales (Cronquist, 1981, 1988; Gibbs; Lindley, 1853; Melchior; Thorne, 1983). These hypotheses, based largely on reproductive features, are also supported by the anatomically similar salt glands of the Frankeniaceae and Tamaricaceae (Solereider) and by the production of D-pinitol by members of both families (Plouvier). A recent novel phylogenetic scheme has the Tamaricaceae in the order Primulales (Goldberg), but this placement is virtually unjustified, except on the basis of such ubiquitous character states as simple perforation plates in xylem vessels, lack of stipules, perfect flowers, superior, unilocular ovaries, and the absence of alkaloids. None of the ordinal characters listed by Goldberg would refute the placement of the Tamaricaceae in the Violales or Tamaricales, and in fact, his description of Primulales requires several qualifiers because of the unusual (for Primulales) character states found in the Tamaricaceae. A cladistic analysis utilizing existing data, or the examination of new lines of evidence, may be required to shed further light on the relationships of this family and, indeed, all of the families of the catchall Parietales.

The basis for the uncertainty in ordinal placement of the Tamaricaceae is the inclusion of two groups of genera (comprising the two tribes Reaumurieae Bentham & Hooker (*Hololachna*, *Reaumuria*) and Tamariceae (*Myricaria*, *Myrtama*, *Tamarix*)⁴) within the family, which at times (e.g., Lindley, 1833, 1853; Maout & Decaisne) have been interpreted as being unrelated. This hypothesized polyphyly is probably based on a misunderstanding of certain character states and their ontogeny. The tribes have been differentiated on the basis of inflorescence structure, distribution of pubescence on the seed, and presence or absence of endosperm in the seed. Developmental studies of the seed have shown that members of the tribe Tamariceae produce cellular (or initially nuclear in *Tamarix tetrandra* Pallas) endosperm, which disappears as the embryo grows to occupy all of the space in the embryo sac (Davis; Puri; Sharma). Thus, the Tamariceae merely show reduction in the development of the endosperm, a trend that correlates with other advanced character states exhibited by the tribe, including tendencies toward elaboration of the hygroscopic hairs on the seed, localization of hairs on the seed, reduction in flower size, increasing complexity of inflorescence architecture, elaboration of the disc, and tetramery in some members.

Members of the Tamaricaceae are generally shrubs or small trees of deserts, sandy or saline areas, shores, riverbanks, and dunes, although some taxa also occur along mountain streams. The branches are covered with small, often scalelike leaves that are punctate with salt-secreting glands. The four- or five-

⁴Several authors (e.g., Bentham & Hooker) have included a third tribe, Fouquierieae, which is generally accorded family status. Its ordinal placement is as unsettled as that of the Tamaricaceae.

[six-]merous, white, pink, or even reddish flowers are quite small but are aggregated into panicles of racemes or spikes that provide spectacular displays. The capsules contain numerous small seeds that may be hairy over the entire surface (tribe Reaumurieae) or have long hairs at the chalazal end forming a conspicuous coma that aids in dispersal (tribe Tamariceae).

Fossils of the Tamaricaceae are very few. *Tamaricoxylon africanum* (Krausel) Boureau, based on fossil wood, is identical in anatomy to modern *Tamarix* (Boureau). The fossils are from northern African Quaternary deposits and thus shed no light on the age of the family. An attribution of Oligocene age to one of these specimens is considered doubtful by Boureau.

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Tamarix Linnaeus, Sp. Pl. 1: 270. 1753; Gen. Pl. ed. 5. 131. 1754.

Shrubs or small trees of shorelines [deserts, steppes] on sands and clays, often in areas of high salinity, with extensive root systems, often also with adventitious roots from buried branches. Leaves herbaceous, small, scalelike, entire, alternate, exstipulate, glabrous or papillose [or hairy], sessile with narrow base or somewhat amplexicaul [or vaginate], with salt-secreting glands. Inflorescence of simple or compound racemes, often paniculately branched, occurring on branches of previous and/or current year's growth. Flowers small, perfect [imperfect], 4- or 5-merous, actinomorphic. Bracts shorter than, equal to, or longer than their subtended pedicels, single [2 or 3 in *Tamarix rosea* Bunge], scalelike, entire, glabrous or papillose [or hairy], sessile with narrow base or somewhat amplexicaul [vaginate] (not necessarily paralleling leaf morphology). Sepals 4 or 5 (6), connate for a short distance near base, entire to denticulate [incised], glabrous or papillose [or hairy], imbricate. Petals 4 or 5 (6), white, pink, or red, ovate or elliptic to obovate, entire to emarginate, equilateral or not, persistent or deciduous after anthesis, contorted in bud. Androecium diplostemonous, the outer whorl of 4 or 5 antesepalous stamens, the inner whorl abortive and developed into a nectariferous hypogynous disc with antepetalous lobes [or of 4–10 antepetalous stamens]; stamens free, inserted onto the central disc; anthers dithecal, usually cordate, apiculate or not. Pollen usually tricolpate (rarely tetracolpate), prolate to spheroidal, [9.5–]11.5–23.5[–26] μm wide, [12.5–]14–28.5[–30] μm long, walls with fine [to coarse] reticulate sculpturing, lumina circular, polygonal or irregularly shaped, clearly defined to the edge of colpi or not. Gynoecium pyramidal or bottle shaped, consisting of 3[–5] carpels, each with a parietal placenta; styles and stigmas 3[–5]. Fruit a loculicidal, many-seeded capsule. Seeds 0.5–0.7 mm long, elongate-obovoid, straight, comose at chalazal end, otherwise glabrous [or hairy near apex]; hairs of coma unicellular, hygroscopic, with wavy thickenings near base; endosperm none. Base chromosome number 12. LECTOTYPE SPECIES: *T. gallica* L.; see Britton, North American Trees, 702. 1908. (The etymology of *Tamarix* is uncertain, but the name is probably derived from the Tambre (Tamariz) River in Spain, although the Tamaro River in Nepal and the Hebrew word *tamaruk* have also been suggested as possible sources.)—TAMARISK, SALT CEDAR.

A genus of about 54 species, of the Middle East, the Mediterranean area, central Asia, and southern Africa. Ten species have been introduced into North America, and six of these are naturalized to varying degrees in the Southeast: *Tamarix gallica* L., *T. ramosissima* Ledeb., *T. canariensis* Willd., *T. africana* Poiret, *T. tetragyna* Ehrenb., and *T. parviflora* DC. The first southeastern records of tamarisks as escapes from cultivation appear to date from 1897 (Horton, 1964).

The infrageneric taxonomy of *Tamarix* has undergone many revisions. Bunge divided the genus into sections on the basis of seasonality of flowering and used numbers of floral parts, raceme and vegetative morphology, filament-insertion patterns, petal persistence, and capsule and style morphology as the basis for further subdivisions. However, Baum (1964) and others have shown

that seasonality of flowering is unreliable and that many species have both vernal and aestival (or continuous) anthesis. One of the most useful sets of characters derives from disc morphology. The three sections recognized by Baum (1978) are characterized by features of the disc, as well as by raceme width, petal length, and stamen number and position. Section TAMARIX generally has racemes less than 5 mm broad, petals 1–2.25 mm long, and five antesealous stamens. Series within this section differ in vegetative features such as the presence or absence of papillae and leaf morphology. Species of sect. OLIGADENIA (Ehrenb.) Endl. have broader vernal racemes, some tetrandrous members, and discs with nectariferous lobes. The series within this section differ in bract length relative to pedicel length, petal shape and length, and raceme morphology. Species of sect. POLYADENIA (Ehrenb.) Baum also have broad racemes but have more stamens and discs that lack nectariferous lobes. Its two subdivisions (ser. ARABICAE Baum, ser. PLEIANDRAE Bunge) differ in the number of antepetalous stamens arising from the disc. The taxa in North America belong to sects. TAMARIX and OLIGADENIA.

Collectors should be aware that most tamarisks are virtually unidentifiable in the vegetative state.

Sect. TAMARIX ser. TAMARIX⁵ is represented in North America by *T. gallica*, French tamarisk (filaments five, arising directly from the lobes of the disc, raceme rachis glabrous, racemes arising mostly from green (new) wood, sepals entire or subentire, petals oval, caducous), and *T. ramosissima* (*T. pentandra* Pallas, *pro parte*, nom. illegit., *fide* Baum, 1978; *T. odessana* Stev. ex Bunge) (filaments five, inserted under the disc between its lobes, sepals denticulate, petals obovate, persistent). *Tamarix gallica* is the most widely recorded species in North America, including our area (Chapman; Jones & Coile; Long & Lakela; MacRoberts; Radford *et al.*; Small, 1913, 1933). However, most of these records are incorrect; the species is actually quite rare in North America. In the Southeast it is naturalized in Georgia, Louisiana, and North Carolina. Its natural range includes France, Spain, Switzerland, Italy, and Sicily. *Tamarix ramosissima*, a halophyte commonly cultivated in Arizona and California, has become naturalized in the Southwest. Its natural range spans central Eurasia from eastern Turkey, the Ukraine, and eastern Iraq eastward to Mongolia, Tibet, central China, and North Korea. In our area it is known from Arkansas, Georgia, Louisiana, Mississippi, North Carolina, and South Carolina.

Sect. TAMARIX ser. LEPTOSTACHYAE (Bunge) Baum is represented in the naturalized flora of North America by *Tamarix canariensis* Willd. (filaments inserted at tips of lobes of disc, with bases dilated, sepals denticulate, rachis of racemes usually papillose). Although Baum (1967) noted that *T. canariensis* had only recently been introduced into Arizona, an examination of specimens from many southeastern herbaria indicates that it has been naturalized in the Southeast since at least 1903. It has been found in North Carolina, South Carolina, Georgia, and Louisiana. The native range of *T. canariensis* is the

⁵Series TAMARIX was called ser. *Gallicae* by Baum (1978), but since it contains the type of the genus, it must be called ser. TAMARIX.

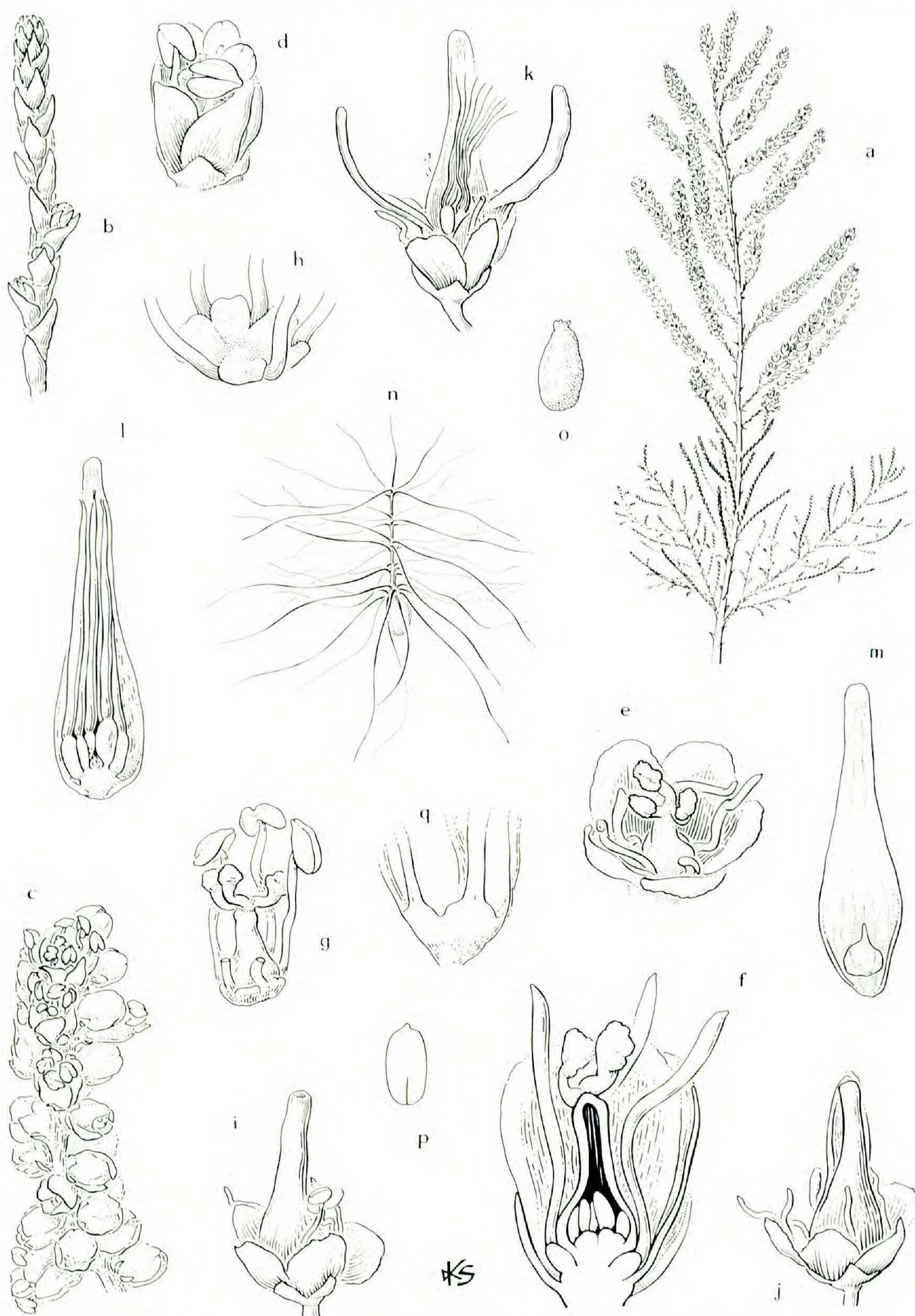


FIGURE 1. *Tamarix*. a-p, *T. ramosissima*: a, tip of branch with inflorescence, $\times \frac{1}{2}$; b, detail of vegetative twig with 2 developing lateral buds, $\times 6$; c, detail of inflorescence, $\times 5$; d, young flower with anthers ready to dehisce, $\times 12$; e, flower after anthers have fallen, the stigmas receptive, $\times 12$; f, flower in vertical section, showing attachment of filaments to disc and of ovules to 2 parietal, basal placentae, $\times 20$; g, gynoecium and androecium removed from flower (upper portions of 2 stamens removed), showing attachment of stamens between lobes of disc, $\times 12$; h, detail of disc and bases of filaments,

western Mediterranean Basin (Sicily, extreme southern France, Sardinia, Spain, Morocco, Algeria, Tunisia, and the Canary Islands). Similar to *T. africana* and *T. gallica*, it differs from the former in its smaller flowers (petals less than 2 mm long, racemes not over 5 mm wide) and its obovate (vs. ovate) petals, and from the latter in its denticulate sepals, papillose raceme rachises, and somewhat expanded filament bases. There appears to be considerable morphological overlap between *T. canariensis* and *T. gallica*, however, and the taxonomic and evolutionary relationships of these two taxa require reevaluation.

Section OLIGADENIA ser. ANISANDRAE Bunge is represented in the Southeast by *Tamarix africana* (stamens five, arising directly from disc lobes, petals relatively large, to 3 mm long) and *T. tetragyna* (antesepalous stamens 4 or 5, arising from lobes of disc, one to several smaller antepetalous stamens also present along edge of disc; sepals denticulate; raceme rachis densely papillose; leaves tending to be amplexicaul; vernal racemes more than 5 cm long, loosely flowered). *Tamarix africana* is naturalized in Louisiana and South Carolina. Its indigenous range includes southern Europe (France and Spain to Italy and Yugoslavia) and northern Africa (Canary Islands and Morocco to Tunisia). Similar to *T. gallica* in disc morphology, it has dilated filament bases. *Tamarix tetragyna*, native to the Middle East (Egypt, Israel, Jordan, Lebanon, Syria, and Cyprus), is reported here for the first time as a naturalized member of the North American flora. It is established on Cumberland Island in Camden Co., Georgia (*W. H. Duncan 29934*, 9 April 1982; DAO). This species differs from all the others that have become naturalized in North America in having antepetalous stamens in addition to the antesepalous ones. It has been the subject of physiological investigations on salt tolerance (see below).

Section OLIGADENIA ser. ARBUSCULAE Baum contains *Tamarix parviflora* (*T. tetrandra* of American authors, not Pallas), small-flowered tamarisk, the only naturalized North American species that is consistently tetramerous and tetrandrous. Its sepals are denticulate and ridged, and its filaments arise directly from the lobes of the disc. Naturalized in Florida, Louisiana, Mississippi, and North Carolina, as well as throughout the Southwest, its natural range includes southern Europe from Corsica to Turkey, and perhaps also Spain and northern Algeria.

In addition, Baum (1967) recorded *Tamarix aphylla* (L.) Karsten (sect. TAMARIX ser. VAGINANTES (Bunge) Bunge), *T. aralensis* Bunge (sect. TAMARIX ser. LEPTOSTACHYAE), and *T. chinensis* (sect. TAMARIX ser. LAXAE Gorshk.) as being naturalized or cultivated in North America. *Tamarix aphylla* is known to be naturalized only in the southwestern United States; it is native to North

gynoecium removed, $\times 20$; i, mature, unopened fruit, with persistent calyx lobes, petals, and filaments, $\times 10$; j, capsule with the 3 valves beginning to separate apically, $\times 10$; k, fully open capsule, 2 seeds still inside, $\times 10$; l, nearly mature capsule with 1 valve removed to show seeds attached to parietal, basal placenta, $\times 12$; m, valve of capsule after shedding of seeds, placenta visible below, $\times 12$; n, wind-dispersed seed with coma, $\times 12$; o, seed body, $\times 25$; p, embryo, oriented as in seed body in "o," $\times 25$. q, *T. canariensis*: detail of disc, showing insertion of filaments on lobes of disc, $\times 20$.

and East Africa, the Middle East, and western Asia eastward to central India. *Tamarix aralensis* has not yet been found as an escape in the Southeast, but it has been grown as an ornamental shrub in Orange Co., North Carolina (*W. C. Coker s.n.*, 2 June 1942; NCU). It is indigenous to the southern Soviet republics of Kazakhstan, Turkmenistan, Tadzhikistan, and Uzbekistan, as well as to Iran and northern Afghanistan. It differs from its close relative, *T. canariensis*, in having filaments that arise from between the lobes of the disc rather than directly from the lobes. *Tamarix chinensis* (*T. pentandra* of American authors, in part, not Pallas; *T. juniperina* Bunge) is widely cultivated in North America. It has been grown in North Carolina (*N. Henry s.n.*, 5 July 1932; NCU), but contrary to Baum's (1967) findings, I have located no authentic record of escape from cultivation in the Southeast. The natural range of *T. chinensis* includes Mongolia, The People's Republic of China, and Japan. It is not a halophyte, unlike most other species of the genus, although it is a xerophyte. Although very similar to *T. ramosissima*, *T. chinensis* has subentire sepals, and in the vernal flowers some of the filaments are inserted between the lobes of the disc on its margin rather than below it. However, in aestival flowers the filament-insertion pattern breaks down. It is difficult to see how these taxa can be recognized as different species, let alone members of different sections of the genus! Both *T. chinensis* and *T. ramosissima* have gone under the name *T. pentandra* in North America, where they are considered to be serious pests along water courses in the deserts of the Southwest. An extensive body of literature on their spread, physiological ecology, and control has developed (see below). One additional species, *T. mascatensis* Bunge (sect. TAMARIX ser. TAMARIX) has been cultivated in Florida and Texas but is not yet known to have escaped.

There are two centers of diversity for the genus. One of these, the Indo-Turanian region, is also said to be its center of origin, with several of the species there exhibiting primitive character states (poorly developed nectariferous disc, large flowers, both as in *Tamarix ericoides* Rottler). A secondary center of diversity exists in the Middle East. Although most species of *Tamarix* are desert or shoreline plants, Vasilchenko & Vasileva argued that the genus may have originated in mesic habitats along mountain streams on what were probably islands in the Tethys Sea during the Paleogene. Their argument is based on the current distribution of *T. arceuthoides* Bunge, which, however, is not one of the more primitive taxa, at least according to Baum (1978). More detailed analyses of the biogeography of the region, and of that time period, will be needed to test their hypothesis.

Brotherson & Winkel have outlined several aspects of the life history of *Tamarix ramosissima* that contribute to its success as a colonizer. These include the ability to produce seeds throughout the growing season and under a wide range of conditions, cross-pollination by wind, self-compatibility when cross-pollination is not effected, high seed output, long- and short-range dispersal capabilities, vigorous vegetative reproduction, allelochemical potential (presumably by way of salt secretion), and wide environmental tolerances. Seed germination can take place at any time during the growing season as long as

sufficient moisture is available. The primary root elongates very quickly after germination.

There is contradictory evidence regarding the mode of pollination in *Tamarix*. Although Brotherson & Winkel suggested that pollination is mediated by wind, floral morphology indicates that entomophily must also occur in some species. The staminal disc secretes nectar, a nutritional reward for potential pollinators. However, within *Tamarix* there has been a trend toward the production of smaller grains of pollen in smaller flowers, which has been interpreted as a tendency toward anemophily (Baum *et al.*, 1971). No experimental investigations of incompatibility systems have been undertaken, and self-compatibility may vary from species to species. It has been reported for *T. ramosissima* and for *Myricaria germanica*, but cultivated material of *T. chinensis* in New York has failed to set seed (R. G. Means, New York State Museum, pers. comm., 1988).

Vegetative modes of reproduction are also important in the spread and persistence of *Tamarix* species. Several species are known to produce adventitious roots and vigorous new shoots from stem tissue that becomes buried. Periodic burning, clearing, or flooding may lead to the development of impenetrable thickets of *Tamarix* (Everitt). Thus, although reproduction from seed may be important, the significance of layering and reproduction from vegetative fragments that have been dispersed along water courses should not be underestimated in the rapid spread and colonization of extensive areas in the Southwest by *T. ramosissima* and other species.

Horton (1964) reviewed the history of the introduction and spread of tamarisks in the United States, and several authors have dealt with the problem of the "weedy" species since then. *Tamarix* "gallica" had become naturalized along the Gulf Coast of Texas by 1877. Its migration into Kansas is well documented. It moved east from Colorado during the 1920's on floods of the Arkansas River and had spread halfway across Kansas by 1939 (Gates). *Tamarix* "pentandra" had become naturalized in North Carolina by 1897 and was first recorded as an escape in Arizona in 1901. Not present in Utah before 1925, it spread rapidly along the major river systems and lake shores between 1935 and 1955. More recently, it has begun to invade mountain streams and reservoirs (Christensen, 1962). It is now a common riparian tree in Utah, Nevada, Arizona, New Mexico, Colorado, and Texas (in Texas, 450,000 acres had been colonized by 1965) and is also known from southern Montana, Idaho, Nebraska, and South Dakota. *Tamarix* "tetrandra" (*T. parviflora*), introduced into the Southwest largely to prevent erosion resulting from overgrazing by livestock, became established in Texas by 1888 and in North Carolina by 1897 (Horton, 1964). This species has also been reported as an escape in Portugal. Numerous other studies document the spread and effects of tamarisks along river systems and in irrigable land in the Southwest.

The weediness of tamarisks, especially in dry areas, stems from their ability to become established by rapid seed germination and quick growth of very extensive root systems where water resources are limited. Once established, the plants may cause reductions in the width of stream channels, which leads

to flooding, as well as to excessive use of limited water supplies (although varying opinions exist on this point; see, for example, Waisel, 1960b).

Tamarix chinensis has the capacity for stomatal closure under conditions of high wind or temperature, thereby diminishing its evapotranspiration rate. In *T. aphylla* diurnal stomatal closure may be mediated by an endogenous circadian rhythm (Hagemeyer & Waisel). Other xeromorphic features of the leaves probably also minimize water loss. In *T. chinensis* stomata appear to respond directly to changes in the leaf-to-air absolute humidity gradient, leading to more efficient water use during the hottest part of the day, when the evaporative demand is greatest.

Tamarisks replace native vegetation and are less attractive to most species in the southwestern avifauna. Only the mourning dove (*Zenaida macroura* (L.)) and the white-winged dove (*Z. asiatica* (L.)) find tamarisk stands to be suitable nesting sites, according to a 1977 report by B. W. Anderson and colleagues, although ladder-backed woodpeckers (*Picoides scalaris* (Wagler)) have since been recorded as nesting in *Tamarix chinensis* in the Southwest.

The salt glands of several species of *Tamarix* have been studied extensively, with the aim of determining mechanisms by which these xerophytes survive in soils with high salt concentrations. Located on both leaf surfaces and young branches, the glands consist of two highly vacuolated and six less vacuolated cells, surrounded by epidermal cells with thickened walls. Numerous plasmodesmata connect the collecting cells with adjacent mesophyll cells. Although Mace believed that there was no association between the salt glands and vascular bundles, later studies of apoplastic transport (e.g., C. J. Campbell & Thomson) indicate that solutes can be shunted from the xylem to the salt gland under conditions of high salinity. The types of salts secreted by these glands vary, depending on the root environment. Both monovalent and divalent cations, including Na^+ , K^+ , Ca^{++} , and Mg^{++} , are present in the solutions. There is no apparent selectivity between cations of the same valence, but divalent cations are prevalent. Anion constitution also varies, with Cl^- , NO_3^- , HCO_3^- , and SO_4^{--} being the major ones. In one investigation HCO_3^- comprised 60 percent of the anion pool (Berry, 1970), and in another SO_4^{--} was predominant (Hem). Salt secretions are sometimes so extensive that columns or cuboidal crystals of salts develop above the gland pores, and concentrations of salts in the secretions may be 20 times greater than those in the local ground water. *Tamarix tetragyna* (and probably other species) has additional physiological adaptations to soil salinity. Tolerance to salinity stress is at least partially mediated by very large amounts of free proline in the roots.

The only investigations of organic natural products in the Tamaricaceae have involved *Tamarix* species. Long-chain alkanes and esters have been partially characterized in *T. gallica*. The alkanes generally contain 18–35 carbons, and the esters have 40–52. Various hydroxylation substitutions occur along these chains, but the level of hydroxylation is very low. The pool of waxy constituents generally contains mixtures of isomers. In *T. "pentandra"* the epicuticular waxes are variable in constitution, with the variability apparently unrelated to ecological factors (Wilkinson, 1980). Several complex or unusual phenolics,

including tannins, a furanofuran, a phenolic glyceride (niloticol), a 3,4-benzocoumarin (a rare class of natural products), a new 4-methylcoumarin, a new digalloylglucose (nilocitin), and several aldehydes, have been isolated from *Tamarix* species. Various flavonoids, including unmethylated, mono-, and dimethyl ethers of the flavonols quercetin (rhamnetin, isorhamnetin, tamarixetin, tamarixin) and kaempferol (kaempferide, rhamnocitrin), as aglycones, glycosides (glucosides, rhamnosides, and glucuronides), and sulfates, have also been found in such tissues as leaves, flowers, and roots. The leaves of all five species of *Tamarix* analyzed contain D-pinitol (Plouvier). In various species the organic acids trans-2-hydroxy-4-methoxycinnamic acid, ellagic acid and its 3,3'-dimethyl ether, gallic acid, and isoferulic acid have been isolated. The systematic significance of most of these compounds has yet to be determined.

There is some evidence of host-specificity among certain gall-forming insects associated with tamarisks. For example, most species of *Psectrosema* (Diptera: Cecidomyiidae) utilize only a single species of *Tamarix*. One species is known to use two hosts; two other species use three. Host specificity is maintained in mixed stands of tamarisks. When more than one species of *Psectrosema* utilizes the same host species, the insects attack different parts of the tree, minimizing competition (Habib; Harris; Kieffer). There is also some suggestion that other insects, such as mirids (Heteroptera) and aphids (Homoptera), are monophagous or oligophagous with regard to *Tamarix* species (Habib *et al.*; Zocchi). Girdling of branches by cicadas (Homoptera) has been noted in Arizona, but vigorous regrowth from below the girdled areas indicates that no measure of biological control is achieved by these insects.

Despite the detrimental effects *Tamarix* species have had on natural ecosystems in North America, some of the same species, as well as others, are economically important in a positive sense. *Tamarix aphylla* and other species are sources of tannins, which are produced in healthy branch, bark, fruit, and leaf tissue, as well as in galls induced by various insects, including moths, scale insects, and gall midges. Tamarisks have also been used for afforestation of dunes and other "unproductive" sandy areas (Decaux; Trabut, 1926; Vilbouchévitch). The wood serves as a source of fuel, charcoal, and construction material, and its ash yields various inorganic salts. Decaux noted that a fine powder of *Tamarix* ash acted as a successful contact insecticide against caterpillars. In Manchuria and Tibet young branch tips of tamarisk have been used to make tea, and in northern Europe tamarisk has served as a substitute for hops in the making of beer. *Tamarix "pentandra"* has been shown to accumulate trace elements such as boron, cadmium, copper, lead, lithium, manganese, molybdenum, nickel, and zinc (Dreesen & Wangen; Shiber), both as surface deposits on leaves and internally, which may mean that the plants could serve as indicators of environmental contamination. Medicinally, species of *Tamarix* have been used in the treatment of infections, hemorrhages, enteritis, rickets, gout, and rheumatism, and as astringents, antiseptics, and diuretics (Vilbouchévitch). Some tamarisks are also prized for the honey produced from their nectar. The biblical "manna" is a gummy exudate composed mainly of carbohydrates secreted by coccids (scale insects) that feed on the

branches of *T. mannifera* (Ehrenb.) Bunge (Maleki & Djazayeri). Several species, including those naturalized in North America, are also grown as ornamentals (Bailey *et al.*).

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